Insect Conservation and Diversity

Insect Conservation and Diversity (2014) **7,** 308–313 doi: 10.1111/icad.12054

Solving the puzzle of *Pringleophaga* – threatened, keystone detritivores in the sub-Antarctic

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Abstract. 1. In the globally significant, lowland terrestrial systems of the sub-Antarctic's South Indian Ocean Province Islands, caterpillars of the flightless moth genus *Pringleophaga* (Lepidoptera: Tineidae) are typically responsible for much nutrient turnover.

2. On Marion Island, *Pringleophaga marioni* is a keystone species for this reason.

3. Rising temperatures have led to increasing populations of introduced house mice, which, in turn, feed extensively on *Pringleophaga* caterpillars.

4. Because of the caterpillars' keystone role, predation by mice is leading to changes in the functioning of the terrestrial system.

5. Given the estimates of an extended life cycle duration for *P. marioni* (and its congeners), that is, two to more than 5 years, an ongoing puzzle is why the species has not shown greater population declines on Marion Island than have been recorded (in some habitats 40–97% in 20 years), given extremely high estimates of predation (*c.* 1% of standing biomass per day).

6. One reason may be inaccurate previous estimates of life cycle duration for the species.

7. Here, we provide a new, quantitative estimate, by rearing caterpillars at different temperature regimes (5, 10, 15 and 5–15 °C), and combining these results with additional data from a prior study, to demonstrate that the life cycle duration for this species is approximately 1 year – half the previous minimum estimate.

8. The new quantitative data provide grounds for improved models for estimating population persistence of this species, and information for models assessing the costs and benefits of conservation interventions such as the eradication of invasive house mice.

Key words. Detritivore, house mouse, life cycle, null point of development, predation, sum of effective temperatures.

Introduction

The South Indian Ocean Province (SIOP) Islands of the sub-Antarctic represent unusual ecosystems that have been accorded considerable conservation significance (de Villiers *et al.*, 2005). Unlike most other cold temperate systems, on these islands terrestrial herbivory is uncommon. No indigenous mammalian herbivores are present, and even among the indigenous invertebrates, herbivory is infrequent (Holdgate, 1977; Chown & Convey, 2007). A monophagous lepidopteran and several weevil species, many of which are algae, lichen and moss feeders, constitute the majority of the insect herbivores (Chown, 1994;

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Klok & Chown, 1998; Vernon *et al*., 1998). In consequence, most primary productivity accumulates as peat, and nutrient recycling and mineralization largely take place via a detritus-based food web (Smith & Steenkamp, 1990). Decomposition is facilitated by the activity of several invertebrate species, among the most significant of which are caterpillars of the flightless moth genus *Pringleophaga* (Lepidoptera: Tineidae), which are abundant on the Prince Edward, Crozet and Kerguelen archipelagos [three species: *P. crozetensis* Enderlein (Crozet Islands), *P. kerguelensis* Enderlein (Crozet and Kerguelen Islands), *Pringleophaga marioni* Viette (Prince Edward Islands)] (Viette, 1949; Crafford *et al*., 1986). Indeed, in the most comprehensively studied system, Marion Island (MI) of the Prince Edward group, caterpillars of *P. marioni* are responsible for substantial increases in nutrient mineralization (on average 17× rates found in their absence) and may process in excess of 100 kg ha^{-1} dry mass of litter per year (Smith & Steenkamp, 1992, 1993). *P. marioni* has therefore been identified as a keystone species, and this role likely extends to other islands given the abundance of *Pringleophaga* spp. there (see e.g. Joly *et al*., 1987).

Because of its keystone role, *P. marioni* has also been recognised as a significant component of the way in which interactions between climate change and biological invasions are affecting many of the SIOP islands (Smith & Steenkamp, 1990; Bergstrom & Chown, 1999). In brief, rising temperatures are leading to increasing populations of introduced house mice, which in turn take *Pringleophaga* caterpillars as preferred prey (Crafford & Scholtz, 1987; Le Roux *et al*., 2002), and this is altering the functioning of local systems (Smith, 2008). Indeed, at the Prince Edward Islands, where mice are found on MI, but not neighbouring Prince Edward Island, substantial differences in *Pringleophaga* population densities have been identified between the islands (Crafford & Scholtz, 1987), and evidence exists of further declines in abundance of *P. marioni* on MI (Chown *et al*., 2002). However, an ongoing puzzle is why *P. marioni* has not become exceptionally rare, especially since mice have alternative prey and therefore, in theory (Holt, 1977), could potentially drive their preferred prey (Smith *et al*., 2002) to extinction. Much of the current evidence suggests that at the very least *P. marioni* should be much more highly threatened by the invasive house mouse than appears to be the case (see e.g. Van Aarde *et al*., 2004): (i) Mice have been present on the islands since at least the 1800s (Cooper, 2008). (ii) Estimates of their daily energy requirements, in combination with the past and present contribution of *P. marioni* caterpillars to their diet, indicate a daily consumption by mice of between 0.3 and 1.3% of caterpillar standing biomass (Rowe-Rowe *et al*., 1989; Smith *et al*., 2002), which is exceptionally high for insects generally (e.g. Cornell & Hawkins, 1995; Hawkins *et al*., 1997; Zalucki *et al*., 2002). (iii) Current estimates of the life cycle duration of *P. marioni* range from 2 to more than 5 years (Crafford *et al*., 1986; Crafford, 1990a), suggesting that annual replacement might be exceptionally slow (Rowe-Rowe *et al*., 1989).

Given that mouse energy requirements on the island are similar to those estimated for other populations of the species (see Smith *et al*., 2002), and that the historic records of mouse presence on the island are verifiable (Cooper, 2008), two key parameters that may help resolve the puzzle are estimates of caterpillar biomass and of the life cycle duration of the species. The former certainly indicate a decline in biomass and density over time in some habitats (between 40 and 97% decline in biomass over 20 years (1977–1997) depending on the habitat, Chown *et al*., 2002), but in others the change is less clear (see data presented by Burger, 1978; van Aarde *et al*., 2004). In consequence, at the heart of the puzzle, or perhaps more analytically, key to understanding likely ongoing impacts and the population persistence of *P. marioni*, is the life cycle duration of the species. Such information is significant for two primary conservation reasons. First, forecasts are for increasing impacts by mice as the climate continues to warm (Smith & Steenkamp, 1990). Although caterpillar development rate will likely increase and life cycle duration decline with increasing temperature, so potentially mitigating some predation impacts, the species is susceptible to high temperatures as we show here (see Results and Discussion). Population modelling to estimate the extent of the likely impact requires information on the life cycle of the species. Second, owing to impacts by mice on birds such as albatrosses (Jones & Ryan, 2010), an eradication programme for these rodents is being contemplated given the efficacy of such interventions elsewhere (e.g. Howald *et al*., 2007). For comprehensive assessments of the impacts of such programmes, population level information on all components of the food web is required (Bergstrom *et al*., 2009; Raymond *et al*., 2011). Thus, resolving the duration of the life cycle of *P. marioni* will not only address a long-standing question about the biology of this species but will also assist with conservation assessments of the outcomes of rodent eradication and its alternatives (the most likely of which is no action, given the costs of such programmes and that most programmes are focused on total eradication). Here, we use new laboratory data and previously collected field data to do so.

Materials and methods

Because of the known recalcitrance of the species in the laboratory (Crafford, 1990b), and the scarcity of adult female moths (Chown *et al*., 2002), first larval instar caterpillars, that is, ~0.01–0.03 g (Crafford, 1990b) were collected (in 2009) from abandoned wandering albatross (*Diomedea exulans*) nests (<20) and tussock vegetation (*c*. 1 ha) near the research station on MI (46°54′S, 37°45′E). The caterpillars were visually identified as first instar based on their small size and this was verified by mass (as above) in the laboratory using a Mettler AE163 balance

(Mettler Toledo, Sandton, South Africa). A first collection was made in July and this was supplemented by a second collection in November. Caterpillars were randomly assigned to controlled temperature chambers (MIR; Sanyo, Osaka, Japan) set at 5, 10, 15 and 5–15 °C (12:12 h, low temperature coinciding ~ scotophase) (n = *c*. 100 per temperature given the difficulty of rearing the species). Photoperiods were established according to the seasonal schedule of Marion Island: that is, 16L:8D for November, December, January; 12L: 12D for February, March, April, August, September and October; 8L: 16D for May, June, July. Individuals were held separately in petri dishes filled with homogenised, moistened material from recently abandoned wandering albatross nests that served as both a food source and shelter. Relative humidity within such petri dishes is *c*. 100%. Caterpillars were provided with a fresh supply of nest material every week and the shelf location of batches of five or less petri dishes were re-arranged once a week to avoid shelf effects. The time at which an individual pupated and if it emerged as an adult was recorded. Most of the trial was conducted at Marion Island, but the latter portion thereof (*c*. 3 months) was completed in South Africa (following return of the caterpillars in their incubators via ship to Stellenbosch, South Africa, with their conditions maintained unchanged throughout).

Generalised linear models (Quasipoisson distribution of errors, because of count data and overdispersion (see Crawley, 2007), as implemented in R2.12.0. (R Development Core Team, 2009)) were used to investigate the influence of temperature treatment on duration of the larval and pupal stages. Although mortality at 15 °C was high, estimates of the lower development threshold (LDT) and sum of effective temperatures (SET) (see Honěk, 1996) were made using individual data and ordinary least squares regression implemented in R.

To obtain additional information, especially on the duration of the pupal and adult stages, the number of eggs laid per female moth and the extent of size variation in the field, previously unpublished data from Crafford (1990b), were also used. In that study, caterpillars of a variety of instars (>50 per instar) were collected in the field (between 1983 and 1984), from which *c*. 20 adult moths were obtained. Both caterpillars and adults were maintained in the laboratory either at 5 °C or at 10 °C in custom-built incubators (described in Klok & Chown, 1997) on a 12:12 L:D cycle. An earlier sampling programme, consisting of the collection of 100, 80 mm diameter cores per month, for a full year from May 1983 to April 1984, from the mire vegetation type (described in Crafford & Scholtz, 1987) also provided caterpillars, which were then subject to head capsule (greatest width in dorsal perspective) measurements using a calibrated ocular micrometer fitted to a Wild M5 stereo microscope (Wild, Heerbrugg, Switzerland), to determine whether the progression of a cohort of individuals in the field could be identified. Here, a runs test (implemented in MS-Excel) was undertaken on the monthly data of the proportional abundance of sampled caterpillars with head capsule widths <1 mm, to determine whether new cohorts appear at random, or whether a run of small, likely first instar (see Crafford, 1990b), caterpillars was sampled.

Results and discussion

In the more recent laboratory study, *P. marioni* larvae took approximately 46–66 weeks to complete their development at 10 °C and 5 °C respectively (Fig. 1). Bearing in mind that laboratory trials commenced with first instar larvae, but that in Lepidoptera this instar is short compared with the others (see e.g. Scoble, 1992; Davidowitz *et al*., 2004), it appears that development is completed at these temperatures in approximately a year. At 15 °C, development was much faster, but mortality was high. Indeed survival in the laboratory was less than 5%, and this has been found in other investigations (T. M. Haupt, unpublished data). Survival was higher at the fluctuating temperatures, and development time was not significantly different to that at 10 °C (compared using a stepwise deletion procedure, see Crawley, 2007, p. 374; also Fig. 1). Bearing in mind high mortality at 15 °C, the LDT and SET estimates were 0.8 °C and 272 degree days respectively. The former is in keeping with findings that the growth of *P. marioni* caterpillars is compromised by long-term exposure to sub-lethal low temperatures, even though they are freezing tolerant (Sinclair & Chown, 2005).

Pupal duration documented by Crafford (1990b) was 52–65 days, with adult females living for 7–11 days and adult males 12–18 days. Females laid 203 eggs with an egg duration of 30–50 days. Soil microclimate recordings

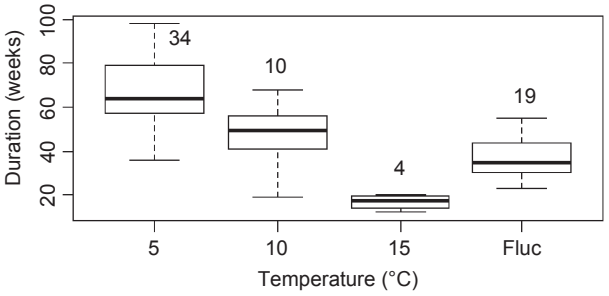

Fig 1. Duration of the larval stage of *Pringleophaga marioni* at 5 °C, 10 °C, 15 °C and a fluctuating temperature of 5–15 °C (Fluc). Sample sizes are indicated above each of the box and whisker plots which indicate the median, quartiles and extremes. Means and standard errors for these data are given in the following: 66.7 ± 14.0 (5 °C), 46.0 ± 15.5 (10 °C), 16.8 ± 3.6 (15 °C) and 37.1 ± 9.8 (fluctuating) weeks. Significant differences were found between the different temperature treatments except for 10 °C and the fluctuating treatment (Generalised Linear Model, Quasipoisson distribution of errors, t = 3.6–13.2, $P < 0.0008$ in all significant cases).

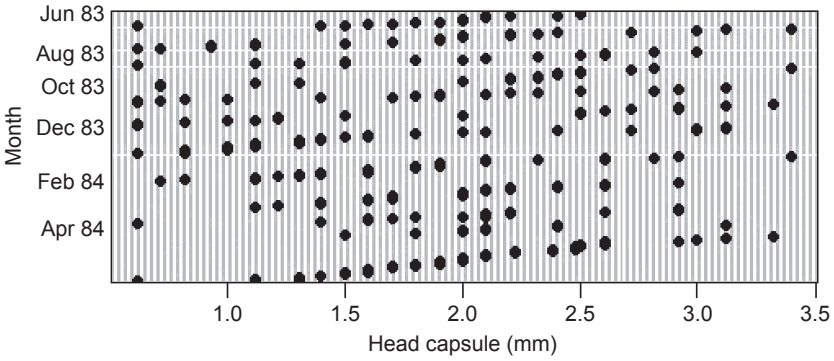

Fig 2. Cleveland dotplot of head capsule measurements of *Pringleophaga marioni* caterpillars collected in a mire plant community between 1983 and 1984. Dots indicate single individuals. Note the scarcity of first instars in the late austral summer and early winter.

from Marion Island, taken at *c*. 50 m a.s.l, indicate that habitat temperatures vary from 3.8 °C (mean minimum) to 8.6 °C (mean maximum) (Deere *et al*., 2006). Summing the duration of the egg, larval and pupal stages, and bearing in mind this temperature range, suggests that *P. marioni* completes its life cycle within one year. Considering that conditions in the field from a nutritional choice perspective (see Simpson & Raubenheimer, 2012) will be more optimal than in the laboratory, and that caterpillars may seek out thermally optimal environments (Sinclair & Chown, 2006), a year-long life cycle is plausible. Head capsule measurements from the 1983–1984 field survey also suggest that cohorts of individuals with a *c*. 1 year interval are present (Fig. 2). In particular, the runs test on individuals with head capsule widths <1.0 mm indicated that the data are non-random [$Z = -2.422$, $P < 0.016$ (two-tailed)]. As a proportion of the total sample for each month, the months of January to June have fewer than 10% of individuals of this size, whereas between July and December the proportion exceeds 10%, peaking at 25% in October, in keeping with a general increase in adult insect activity on the island in early spring (e.g. Chown & Scholtz, 1989).

A year-long life cycle for *P. marioni* is at least half as long as that previously estimated (Crafford *et al*., 1986) and may go some way to explaining why the species has not declined to very low numbers on Marion Island. That is, population replacement is faster than has previously been assumed. The finding does not mean, however, that *P. marioni* is not at substantial risk from mouse predation, given that it remains a preferred prey species (Smith *et al*., 2002) and census estimates indicate a declining population (Chown *et al*., 2002). Nonetheless, the new estimate of life cycle duration will make formal models of population persistence more accurate, and will also facilitate modelling of the outcome of various possible conservation interventions (from none to full eradication of mice). In the former case, and given the restricted distribution of the species (only Marion and Prince Edward Islands), the potential now exists for formal assessment of the species according to the IUCN red list criteria. To date, no such assessments have been made for plants or invertebrates in the sub-Antarctic.

The information provided here will also contribute to improved understanding of the genetic structure of the species on the island (and the two *Pringleophaga* species found on the other islands, see Viette, 1949; Paulian, 1953) because of better estimates of divergence times among locations (see Groenewald *et al*., 2011), which depend on estimates of life cycle length. The current findings also contextualise the species in the polar, and especially the sub-Antarctic, insect fauna more generally (Vernon *et al*., 1998). That is, they have a year-long life cycle, as do many other sub-Antarctic species, such as the ectemnorhine weevils (Chown, 1994), but they have a relatively brief adult stage. This makes them most similar to the 'Category 1' species with long life cycles discussed by Danks (1992). Although a year-long life cycle is relatively compressed compared with insects such as the 17-year cicada, some wood feeding beetle species, and several other polar taxa (Danks, 1992; Convey, 1996), it is still much longer than is typical for most insects (Fig. 3).

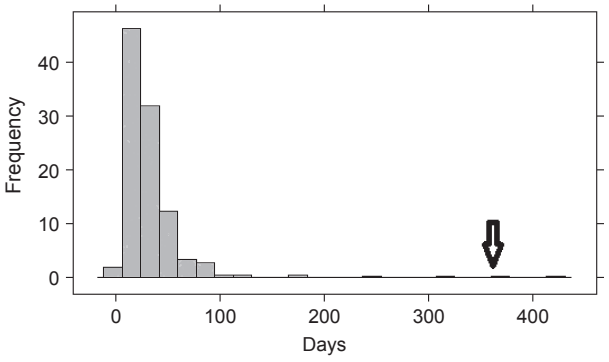

Fig 3. Histogram of development times (days) of insects at their average habitat temperature (typically 20–25 °C) from the data compiled by Irlich *et al*. (2009) (here $n = 501$ and frequency is %), indicating the location of *Pringleophaga marioni* at 10 °C (arrow). The record life cycle duration for insects (not shown on the histogram) is *c*. 17 years or >6200 days.

Acknowledgements

This study was funded by South African National Research Foundation grant SNA2007042400003 and by an NRF special merit bursary to TMH. The South African National Antarctic Programme provided logistic support in the field. Field research by JEC was supported by the University of Pretoria. We thank three anonymous reviewers for helpful comments on a previous version.

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Accepted 31 July 2013
First published online 27 August 2013

Editor: Simon R. Leather
Associate editor: Robert Ewers